Host Breadth and Parasitoids of Fruit Flies (*Anastrepha* spp.) (Diptera: Tephritidae) in Puerto Rico

DAVID A. JENKINS[1] AND RICARDO GOENAGA

USDA–ARS, Mayaguez, Puerto Rico 00680-5470

ABSTRACT   Twenty fruit species representing 12 families were collected from various regions in western Puerto Rico and monitored for the emergence of *Anastrepha* spp. pupae. We collected 14,154 tephritid pupae from 16 fruit species representing 10 families. The relative infestations of these fruits (pupae per kilogram of fruit) were recorded. Recorded host ranges were not in complete agreement with those reported in the literature. This host-use pattern should give pause to regulators of fruit importation and exportation that base their decisions on literature from regions other than those of immediate interest to them. We recovered the braconid parasitoid *Utetes anastrephae* (Viereck) from tephritid pupae collected from *Mangifera indica* L., *Spondias mombin* L., *Psidium guajava* L., *Chrysobalanus icacos* L., *Terminalia catappa* L., and *Garcinia intermedia* (Pittier) Hammel. We collected one specimen of the parasitoid *Doryctobracon aerolatus* (Szepligeti) from the west coast (Añasco), which had not been previously reported in Puerto Rico. We present a preliminary phenology of what are probably the primary fruit hosts of the *Anastrepha* spp. of Puerto Rico. We also present the first report of *Garcinia intermedia* (Pittier) Hammel and *Coffea arabica* L. as reproductive hosts of *A. suspensa*.

RESUMEN   Se colectaron frutas de 20 especies de árboles frutales, representando 12 familias botánicas, de varias localidades en Puerto Rico y se monitorearon para detectar la presencia de pupas de *Anastrepha spp.* Se logró colectar 14,154 pupas *Tephritidae* de frutas correspondiente a 16 especies y 10 familias botánicas. Las infestaciones relativas de estas frutas (pupas/kg fruta) fueron registradas. Los hospederos de *Anastrepha. spp.* encontrados en esta investigación fueron inconsistente con aquellos reportados en la literatura. El patrón de uso encontrado en este estudio de *Anastrepha spp.* para sus hospederos debe alertar a las agencias encargadas de regular la importación y exportación de frutas a tomar sus decisiones en base a la literatura proveniente de la región de interés y no de otras regiones similares reportadas en la literatura. El parasitoide *Utetes anastrephae* (Viereck) fue recobrados de pupas colectadas de *Mangifera indica* (L.), *Spondias mombin* (L.), *Psidium guajava* (L.), *Chrysobalanus icacos* (L.), *Terminalia catappa* (L.) y *Garcinia intermedia* (Pittier) Hammel. Se colectó un espécimen del parasitoide *Doryctobracon aerolatus* (Szepligeti) de la costa oeste (Añasco), que no había sido reportado anteriormente en Puerto Rico. Se presenta en este reporte una fenología preliminar de los principales frutales que pueden servir de hospederos a *Anastrepha spp.* en Puerto Rico. También se reporta por primera vez a *Garcinia intermedia* (Pittier) Hammel y *Coffea arabica* (L.) como hospederos en la reproducción de *A. suspensa*.

KEY WORDS   *Anastrepha obliqua*, *Anastrepha suspensa*, *Mangifera indica*, *Utetes anastrephae*

Fruit flies in the family Tephritidae are often pests of economically important fruit (White and Elson-Harris 1992). Because species may be transported to other areas in infested fruit, regulatory agencies from many countries have applied importation policies that severely restrict the import of fruit (Cowley et al. 1992).

One tool regulatory agencies rely on is the literature of reported hosts for fruit flies in countries or regions wishing to export their fruit. One easily available survey of this literature is the Fruit Fly (Diptera: Tephritidae) Host Plant Database (Norrbom 2004), although this is limited to New World tephritids. Although valuable tools, many reports of host use by economically important tephritids are not reliable. Some data refer to flies reared on fruit in laboratory studies and not from field-collected fruit. Many are secondary accounts (citations of previous literature) or misidentification of the host and/or fly species,
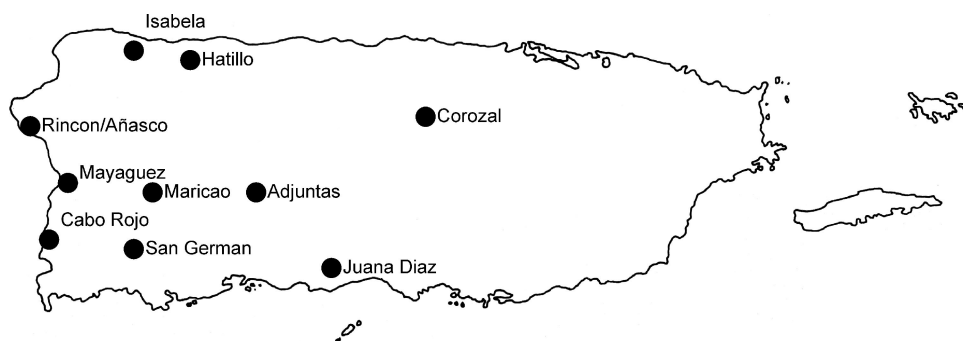

Fig. 1. Map of Puerto Rico with regions where collections were obtained. Fruit was often collected from multiple sites within each region.

particularly in older literature where hosts are identified by common names. Of the 14 citations of the host status of *Pouteria sapota* (Jacq.) H. E. Moore and Stearn (Sapotaceae) to *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) in Norrbom (2004), all are either uncertain references or are citations of uncertain references. A recent survey of >1,100 *P. sapota* fruit was unable to detect infestations of *A. obliqua* (Jenkins and Goenaga 2007). (Cowley et al. 1992 reported that evaluating 1,000 fruits "yields 95% confidence that infestations levels >0.3% would be detected.") Furthermore, reliable reports from one region may not apply to another, even adjacent, region. Although *A. obliqua* is reported to infest *Citrus* spp. (Rutaceae) (Enkerlin et al. 1989), this fly has never been recovered from *Citrus* spp. in Cuba, Guyana, or Trinidad and Tobago (White and Elson-Harris1992). Similarly, *A. obliqua* is an important pest of mango, *Mangifera indica* L. (Anacardiaceae) in the Caribbean but has never been recovered from this fruit in Trinidad or St. Lucia (White and Elson-Harris 1992). Such inconsistent host use patterns (populations of fruit flies having different host preferences in different regions) are suggestive of a geographical segregation of populations throughout the Caribbean islands with a resulting geographical variation in host preferences. Although recent research does not support this hypothesis for *A. suspensa* (Boykin et al. 2006), the locus selected (COI) may not have had enough sequence variation to provide the necessary resolution to detect genetic differences on the geographical level.

A variety of tropical fruit crops are grown in Puerto Rico, and local growers are eager to expand their market to include the continental United States. However, there are currently two economically important species of *Anastrepha* in Puerto Rico, and one of these, *A. obliqua* (Macquart), is only occasionally found in Texas, but is otherwise absent from the continental United States (Epsky et al. 2003). Seín (1933) reported that *A. obliqua* (=*A. fraterculus* Wied., variety *mombinpraeoptans*) and *A. suspensa* (Loew) (=*A. unipuncta* Seín) were found in Puerto Rico. The extensive catalog of the insects of Puerto Rico of Wolcott (1948) and the catalog of the host plants of insects in

Puerto Rico of Martorell (1976) also list only the two species of *Anastrepha* that Seín reported. More recently, on the island of Vieques, Puerto Rico, *A. maculata* (Norrbom) has been recovered from fruits of *Terminalia catappa* L. (Combretaceae), *Mangifera indica*, *Spondias purpurea* L. (Anacardiaceae), *S. dulcis* S. Parkinson (Anacardiaceae), and *Bursera simaruba* L. Sarg. (Burseraceae) (R. Boyle, personal communication). Mrs. Boyle also reported that *A. interrupta* Stone has been recovered from *T. catappa* and *Coccoloba uvifera* (L.) L. (Polygonaceae) on Vieques. *Anastrepha edentata* Stone is also reported from Puerto Rico but its hosts are unknown (Norrbom 2004).

Knowledge of host range of these pests and phenology of their hosts are valuable to growers and regulators alike. A survey of *Anastrepha* spp. and their parasitoids also provides a baseline for future introductions of biocontrol organisms, such as parasitoids, and the introduction of exotic fruit fly species not yet recorded from the island of Puerto Rico. The objectives of this study were to (1) survey a broad sample of fruit species in Puerto Rico for infestations by *Anastrepha* spp., (2) determine the relative density of *Anastrepha* spp. pupae (pupae recovered per kilogram of fruit) in different species of infested fruit, and (3) determine the extent of parasitization of *Anastrepha* spp. in Puerto Rico.

Materials and Methods

Fruit, when available, were collected weekly from multiple sites around the western half of Puerto Rico. Sites fell into 1 of 10 regions (Fig. 1; Table 1). All collected fruit was abscised, except *Manilkara zapota* Van Royen (Sapotaceae) and *Coffea arabica* L. (Rubiaceae). Fruit in the *M. zapota* orchard available to us was harvested by the proprietor before it dropped, so we were obliged to use harvested mature fruit in our study. Coffee berries typically do not abscise, and therefore we collected them straight from the bush when they were ripe (red in color). The species, number, and weight of fruit collected was recorded. Collected fruit was stored on a wire mesh (8 by 8-mm pores) over a plastic bin (40 by 60 cm) containing vermiculite to the depth of 3 cm. The bins were cov-

Table 1. Regions from which fruit were collected with precipitation and elevation

Region	Annual precipitation (mm)	Elevation (m)
Maricao	2,428	450
Adjuntas	1,871	450
Corozal	1,831	195
Rincon/Aasco	1,771	20
Mayaguez	1,744	24
Isabela	1,583	126
Hatillo	1,296	5
Cabo Rojo	1,180	75
San German	1,143	114
Juana Diaz	914	21

ered with ventilated lids to prevent the escape of larvae. Vermiculite was checked every other day for the presence of tephritid pupae. Pupae were placed in plastic petri dishes with a small amount of lightly moistened vermiculite. Petri dishes were stored in an environmental chamber (12:12 L:D) at 25°C. A plastic dish of water was placed in the chamber to maintain humidity. Petri dishes were checked daily for the emergence of adult flies for 30 d. After 30 d, petri dishes were checked monthly for a year (if collected in 2005) or discarded (if collected in 2006 or 2007). Flies were identified using an interactive web-based key (Carroll et al. 2002). The sex and species of the flies were recorded. They were stored in alcohol as voucher specimens at the USDA–ARS Tropical Agriculture Research Station in Mayaguez, Puerto Rico.

Phenology of fruiting was based on when we saw ripe fruit at all locations during our weekly collecting trips.

Results

Amount of fruit evaluated and insects recovered are presented in Table 2. Only four of the fruit species surveyed yielded no tephritid pupae: *Garcinia mangostana* L. (Clusiaceae); *Flacourtia inermis* Roxb. (Flacourtiaceae); *Phoenix dactylifera* L. (Arecaceae); and *Lansium domesticum* Corr. (Meliaceae). Although we reared *A. obliqua* (4,712 adults) and *A. suspensa* (1,654 adults) from many species of hosts (Table 2), three fruit species produced >100 pupae/kg fruit: *Spondias mombin* L. (Anacardiaceae) (exclusively *A. obliqua*); *Eugenia uniflora* L. (Myrtaceae) (exclusively *A. suspensa*); and *Chrysobalanus icacos* L. (Chrysobalanaceae) (mostly *A. suspensa* with a few *A. obliqua*).

The mean yield of pupae per kilogram of *M. indica* was similar for both years (2005 = 11 ± 3 [SEM], 31 collections; 2006 = 9 ± 3, 48 collections). Because we collected *M. indica* fruit on so many different occasions (79), each collection consisting of between 10

Table 2. Fruit species collected and the no. pupal and adult *Anastrepha* spp. and parasitoids yielded

| Fruit species	Locations	Fruit (no.)	Weight (kg)	Pupae (no.)	Mean pupae/kg fruit ± SEM	Adult *A. obliqua*	Adult *A. suspensa*	*Utetes anastrephae*
Anacardiaceae								
Mangifera indica L.	47	1,637	295.48	2,733	9 ± 2	1,258	0	17
Spondias mombin L.	6	1,396	11.69	4,421	378 ± 46	2,104	0	20
Spondias dulcis Forst.	4	152	18.25	65	4 ± 1	5	0	0
Spondias purpurea L.	3	732	12.47	897	72 ± 24	566	18	0
Anacardium occidentale L.	3	70	3.34	7	2.1 ± 1	5	0	0
Myrtaceae								
Psidium guajava L.	2	256	26.77	1,806	67 ± 17	156	510	2
Syzygium malaccense Merr. and Perry	8	303	15.19	180	12 ± 4	62	14	0
Eugenia uniflora L.	1	659	2.17	363	168 ± 39	0	239	0
Clusiaceae								
Garcinia intermedia (Pittier) Hammel	1	826	4.72	71	15 ± 7	0	55	1
Garcinia mangostana L.	1	100	1.80	0	0	0	0	0
Flacourtaceae								
Flacourtea inermis Roxb.	1	389	2.49	0	0	0	0	0
Dovyalis caffra Warb.	1	39	1.34	6	45 ± 42	0	6	0
Oxalidaceae								
Averrhoa carambola L.	4	3,816	423.31	1,390	3 ± 0.4	548	0	0
Combretaceae								
Terminalia cattapa L.	22	2,038	41.53	2,084	50 ± 9	5	736	3
Rutaceae								
Citrus sinensis Osbeck	2	203	34.52	4	0.12 ± 0.2	1	0	0
Rubiaceae								
Coffea arabica L.	1	1,283	2.33	17	7 ± 6	0	9	0
Sapotaceae								
Manilkara zapota van Royen	1	258	43.55	1	0.02 ± 0.04	0	0	0
Chrysobalanaceae								
Chrysobalanus icaco L.	1	498	0.70	113	161 ± 29	4	67	3
Arecaceae								
Phoenix dactylifera L.	1	192	1.26	0	0	0	0	0
Meliaceae								
Lansium domesticum Corr.	1	50	1.24	0	0	0	0	0
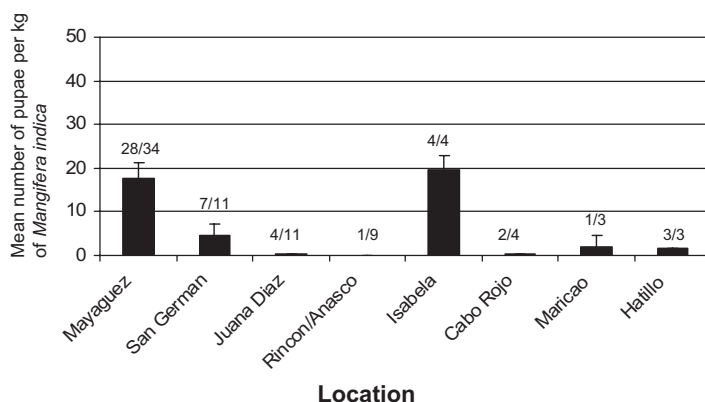
Fig. 2. Mean number (±SEM) of tephritid pupae per kilogram of mango from eight different regions. In the fraction above the bar, the denominator equals the number of collections made in that region, and the numerator equals the number of collections yielding tephritid pupae.

and 45 mangoes, with an average of 22.11 ± 0.82, it was useful to look at the distribution in time and space of collections that yielded no tephritid pupae. Of the 79 collections of mango, 31 collections yielded no tephritid pupae. One of the 4 collections in May 2005 yielded no tephritid pupae; 2 of the 12 collections in June 2005 yielded no tephritid pupae; 1 of the 8 collections in July 2005 yielded no tephritid pupae; the single collection from April 2006 yielded no pupae; 18 of the 28 collections in May 2006 yielded no tephritid pupae; 5 of the 18 collections from June 2006 yielded no pupae; and 2 of the 4 collections in January 2007 yielded no tephritid pupae. In addition to the collections listed above, one collection was made in August 2005, two collections were made in September 2005, and one collection was made in January 2006, all of which produced tephritid pupae. The proportion of collections yielding tephritid pupae is shown in Fig. 2. The mean number of pupae per kilogram of *M. indica* fruit varied widely among the different locations, with sites located in the Mayaguez and Isabela regions yielding more than twice as many pupae per kilogram than fruit collected from the other regions (Fig. 2).

The mean yield of pupae per kilogram of *S. mombin* was higher in 2006 than 2005 (2005 = 245 ± 84, 5 collections; 2006 = 456 ± 54, 14 collections). Every collection of this fruit produced tephritid pupae. The mean yield of pupae per kilogram of *S. purpurea* was higher in 2006 than in 2005 (2005 = 44 ± 11, four collections; 2006 = 144 ± 51, six collections). Every collection of this fruit produced tephritid pupae. Of the nine collections of *S. dulcis,* only three yielded tephritid pupae (because so few collections were infested, no comparison of means is available between years).

All 10 collections of *Syzygium malaccense* Merr. and Perry (Myrtaceae) yielded tephritid pupae. However, only two of these collections occurred in 2005, so no comparison of means between years is available. The mean number of pupae yielded per kilogram of *Psidium guajava* L. (Myrtaceae) was higher in 2006 than in 2005 (2005 = 36 ± 10, seven collections; 2006 =

134 ± 20, three collections). We collected 256 *P. guajava* fruits from two sites in two regions (Adjuntas and Mayaguez). All collections of *P. guajava* yielded tephritid pupae. We collected 659 fruit of *E. uniflora,* all from a single tree in Mayaguez on four occasions in 2006.

The mean yield of pupae per kilogram of *A. carambola* L. (Oxalidaceae) was similar for both years (2005 = 2.5 ± 0.4, 74 collections; 2006 = 3.2 ± 0.7, 43 collections). Of 117 collections of carambola, 34 yielded no tephritid pupae. There was not much variation in pupae per kilogram of fruit between the four regions *A. carambola* was collected from, although fruit from Juana Diaz typically had lower densities of pupae than the other regions (Fig. 3). The mean number of pupae per kilogram of *A. carambola* for all four sites was within the range observed for the mangoes in low-yield locations (San German, Juana Diaz, Rincon/Añasco, Cabo Rojo, Maricao, and Hatillo) (Figs. 2 and 3). Analysis indicated that the average density of tephritid pupae per kilogram of fruit collected from October to February ($n = 50$) was higher (mean = 4.8 ± 0.7) than the average density of pupae per kilogram of fruit collected from March to September ($n = 47$; mean = 0.8 ± 0.2; two-tailed *t*-test; df = 95; $t = 5.6$; $P < 0.0001$).

All *C. icacos* were collected from a single tree in Mayaguez in 2006. All four collections of this fruit yielded tephritid pupae.

The mean number of pupae yielded per kilogram of *T. catappa* by season was as follows: winter 2006/ 2007 = 57 ± 17, 10 collections; summer 2006 = 142 ± 154, 2 collections; winter 2005/2006 = 27 ± 10, 22 collections; summer 2005 = 23 ± 10, 5 collections. We collected *T. catappa* fruits from 22 sites in five regions (Mayaguez, Corozal, Rincon/Añasco, Cabo Rojo, and Isabela). Of 39 collections of *T. catappa*, 8 yielded no tephritid pupae. There seems to be a great deal of variation with respect to infestation of this fruit at different locations (Fig. 4).

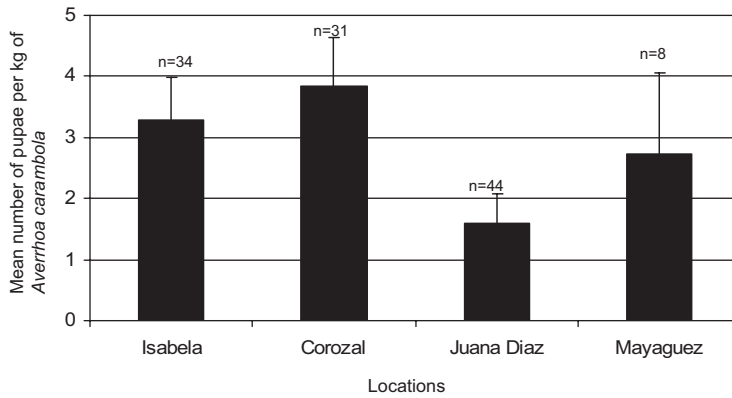The mean number of pupae yielded per kilogram of *Garcinia intermedia* (Pittier) Hammel (Clusiaceae)

Fig. 3. Mean number (±SEM) of tephritid pupae per kilogram of carambola from four different regions. *n*, number of collections from that region.

by year was 7 ± 5 (three collections) and 20 ± 15 (four collections) for 2005 and 2006, respectively. All fruit were collected from a single tree in Mayaguez on seven occasions.

We collected 2,328 *C. arabica* berries from several trees in Adjuntas, all in 2006. Of seven collections of *C. arabica* berries, only three yielded tephritid pupae.

We collected 39 fruit of *Dovyalis caffra* Warb. (Flacourtaceae) from a single tree in Mayaguez on two occasions in 2006.

We collected 203 *Citrus sinensis* Osbeck (Rutaceae) fruit from a number of trees at two sites: Corozal and Adjuntas.

Of eight collections of *Anacardium occidentale* L. (Anacardiaceae) from Mayaguez (two sites) and Cabo Rojo (one site), only one collection from Mayaguez produced any pupae. All eight collections were made during the summer months.

We recovered 17 *Utetes anastrephae* (Viereck) (Hymenoptera: Braconidae) parasitoids from pupae collected from mango fruits, all collected in Mayaguez or Isabela. Twenty *U. anastrephae* emerged from pupae collected from *S. mombin*, all from fruits collected from Mayaguez, Añasco, or Hatillo. Two *U. anastrephae* emerged from pupae collected from *P. guajava*: one from fruit collected in Adjuntas and one from fruit collected in Mayaguez. Three *U. anastrephae* emerged from pupae collected from *C. icacos*, all from fruit collected from Mayaguez. We recovered three *U. anastrephae* from these pupae and one *Doryctobracon areolatus* (Szépligeti) (Hymenoptera: Braconidae). This is the first report of *D. areolatus* in Puerto Rico. *D. areolatus* had been released 1 or 2 mo before as a biological control agent for *Ananstrepha* spp. ~1 mi from the site we collected these fruit (Añasco). One adult *U. anastrephae* emerged from pupae collected from *G. intermedia*. Fruit yielding *U. anastrephae* were collected from the western north coast (Isabela and Hatillo), the west coast (Mayaguez and Añasco), and the mountainous center of the island (Corozal and Adjuntas). No parasitoids emerged from pupae collected from fruits of *A. carambola*, *C. arabica*, S. *malaccense*, S. *purpurea*, or S. *dulcis.*

Discussion

This survey reveals a broad host range of *Anastrepha* spp. in west/west central Puerto Rico: only 4 of the 20 fruit species collected did not yield tephritid pupae, and this may be attributable to inadequate sampling
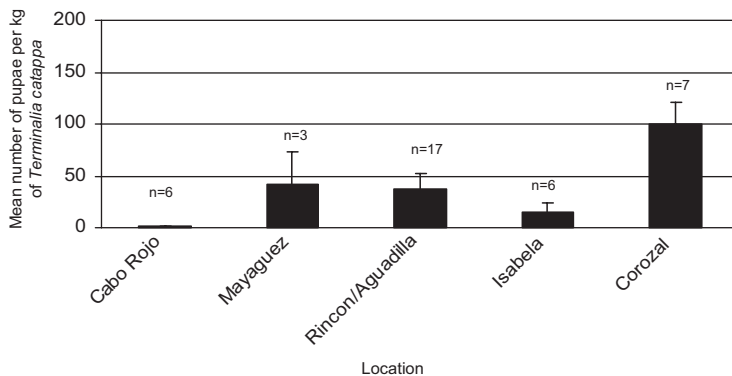

Fig. 4. Mean (±SEM) of tephritid pupae per kilogram tropical almond from five different regions. *n*, the number of collections from that region.

(too few fruit collected or collected from a single location). We observed wide ranges of densities of pupae in hosts among different host species and different locations. The different densities of pupae in different host species may reflect host preference and/or availability of the hosts in time and space. It is also possible that the different densities observed were the result of differential survival of larvae in different species of fruits, although we do not think this is likely. The different densities of pupae in the same hosts in different areas may reflect variations in fruit fly abundance among these locations, especially when a location yields low numbers of fruit flies for multiple host species. For instance, yields of fruit fly pupae per kilogram of *M. indica* and *A. carambola* were extremely low in Juana Diaz (Figs. 2 and 3). Yields of fruit fly pupae per kilogram of *M. indica* and *T. catappa* were low in fruit collected from Cabo Rojo (Figs. 2 and 4). These regional differences in pupal densities may also reflect varietal differences among host fruit. For instance, most *M. indica* collected in the Mayaguez area were the naturalized Mayaguezano variety, whereas all *M. indica* fruit from Isabela were Winters variety. *M. indica* at other locations were different varieties, based on observations of color, shape, and size of fruit, but their identities were not determined.

Although relatively few pupae per kilogram of *M. indica* were produced (Table 2), this fruit is widely available in the summer months and should be considered an important host of *A. obliqua*. *M. indica* is widespread throughout Puerto Rico but does not fruit reliably in the mountainous interior of the island, probably because of winter rainfall in the center of the island. *M. indica* flowers in the winter, so rainfall during this time reduces pollination and, more importantly, facilitates fungal infection, aborting flowers and fruits (Morton 1987; American Phytopathological Society 1998). We saw fruit, albeit small numbers, on *M. indica* trees in Adjuntas and Corozal, wet areas, in May 2007, but none in 2006 or 2005. Observations of 20 trees revealed that 9 *M. indica* trees produced fruit every other year, and 11 *M. indica* trees fruited every year, although it is possible there was an annual fluctuation in yield for these trees. There were a few trees in the dry district of Juana Diaz, which fruited twice in a single year (winter and summer) and fruited again the next year. This was also true for three trees on the northern coast in Hatillo. Although many trees fruited every other year during this study, *M. indica* from naturalized trees were widely distributed both years. This is an important host of *A. obliqua* and potentially of its parasitoids. *M. indica* was recorded as a host of *A. obliqua* in Puerto Rico by Seín (1933) and in other locales (Eskafi 1990, Aluja et al. 2000, Haji and da Gama Miranda 2000, among others). *M. indica* is also reported to be a host of *A. suspensa* (Weems 1965, Swanson and Baranowski 1972, Windeguth et al. 1972).

Native to the Neotropics, *S. mombin* seems to be widespread throughout Puerto Rico, and it fruited every year in the summer (based on nine trees). Two trees in Hatillo fruited in the summer and again in the

winter. *S. mombin* is recorded as a host of *A. obliqua* in Puerto Rico by Seín (1933) and in other locales (Aguiar-Menezes and Menezes 1997, Aluja et al. 2000, Uchôa and Zucchi 2000). It is also listed as a host of *A. suspensa* (Stone 1942, Korytkowski and Ojeda Peña 1970).

Native to the Neotropics, *S. purpurea* is widespread in Puerto Rico, but we have never been able to collect ripe fruit from trees located in the mountainous interior of the island. Trees fruited every year in the late summer, usually after *M. indica* and *S. mombin* have finished fruiting. This is an important host of *A. obliqua*. *S. purpurea* is recorded as a host of *A. obliqua* in Puerto Rico by Seín (1933) and in other locales (Stone 1942, Wasbauer 1972, Eskafi 1990, Aluja et al. 2000, Uchôa and Zucchi 2000). It is also reported to be a host of *A. suspensa* (McAlister 1936).

Native to Asia, *S. dulcis* has a long fruiting season, with fruit remaining on the trees from September into February of the following year. Yields seem to vary in alternate years. This tree is widespread throughout Puerto Rico, often grown in front of homes. Seín (1933) reports that *S. dulcis* is "rarely" a host of *A. obliqua* in Puerto Rico. It is reported to be a host of *A. obliqua* in other locales (Wasbauer 1972, Araujo et al. 2000, Haji and da Gama Miranda 2000, Souza Filho et al. 2000, Veloso et al. 2000) and is reported to be a host of *A. suspensa* in Puerto Rico (Martorell 1976) and in other locales (Swanson and Baranowski 1972).

Native to Asia, *S. malaccense* fruited every year during the summer (based on five trees). However, we found four trees that flowered and fruited in December and January, respectively. There trees also fruited the following July. The four trees were in close proximity to one another (within a kilometer) on a mountain road between Lares and Adjuntas. We also found two trees, one in the town of Lares and the other in the town of Isabela, which fruited in April. Trees in the mountains flowered and fruited 2 or 3 wk later than individuals located at low elevations. This tree is found throughout Puerto Rico but is rarer in the arid southern districts. This is an important host of *A. obliqua*, although *A. suspensa* also uses it. *S. malaccense* is recorded as an "occasional" host of *A. obliqua* and a host of *A. suspensa* in Puerto Rico by Seín (1933). In other locales, *S. malaccense* is reported as a host of *A. obliqua* (Stone 1942, Wasbauer 1972, Aluja et al. 1987, Molineros et al. 1992) and of *A. suspensa* (Martorell 1976, van Whervin 1974).

Native to Southeast Asia, *A. carambola* can produce fruit almost all year long (based on 10 trees). All of our trees were on experimental stations, and we do not know how widespread this species is in Puerto Rico. We also observed significant differences in infestation densities in carambola in different seasons. There are no prior records of *A. carambola* as a host of *A. obliqua* in Puerto Rico, although both *A. obliqua* and *A. suspensa* are reported to use *A. carambola* as a host in the literature (Stone 1942, Swanson and Baranowski 1972, Wasbauer 1972, Boscán de Martínez et al. 1980, Steck et al. 1990, Bressan and da Costa Teles 1991, Silva et al. 1996, Aguiar-Menezes and Menezes 1997, Veloso et al.

2000, Oliveira et al. 2000, Haji and da Gama Miranda 2000, Uchôa and Zucchi 2000, Uchôa et al. 2002).

Native to the Neotropics, *P. guajava* is the only host where we find considerable numbers of both species, although *A. suspensa* predominates. This tree fruits once a year in the summer (based on five trees) and is presumably widespread as a backyard tree. Seín (1933) reports that guava is an important host of *A. suspensa* and an "occasional" host of *A. obliqua* in Puerto Rico.

Eugenia uniflora is native to the Neotropics and fruits heavily once a year during the summer (based on one tree), although we did observe sporadic and very low yield fruiting at other times. It is unclear how abundant this tree is. *E. uniflora* has not been reported as a host of *Anastrepha* spp. in Puerto Rico before this survey. However, it is reported to be a host of both *A. suspensa* and *A. obliqua* in the literature (McAlister 1936, Stone 1942, Weems 1965, Swanson and Baranowski 1972, Wasbauer 1972, Windeguth et al. 1972, Aluja 1984, Eskafi 1990, Couturier et al. 1993, Silva et al. 1996, Fernández et al. 1998, Souza Filho et al. 2000, Veloso et al. 2000).

Chrysobalanus icacos has the distinction of being the only host we found that is thought to be native to Puerto Rico (Liogier 1985). It fruits once a year in the summer (based on one tree). Although it is native to the island, it is unclear how abundant this tree is. Seín (1933) reported that *C. icacos* was a host of *A. suspensa.*

Terminalia catappa is native to Asia and is probably the most widespread tree in our survey, being found in almost all parts of the island, although somewhat rarer in the arid south than in the moister districts. Trees fruited twice a year; once in winter and once in the summer. This is an important host of *A. suspensa* and its parasitoids. Seín (1933) reported that tropical almond was a host of *A. suspensa.* Tropical almond has been reported as a host of *A. suspensa* (Stone 1942, Swanson and Baranowski 1972, Windeguth et al. 1972, van Whervin 1974) and of *A. obliqua* (McAlister 1936, Wasbauer 1972, Souza Filho et al. 2000).

Garcinia intermedia is native to Asia and typically fruits once a year in the summer, but we did observe the tree to fruit in January 2007. The duration of fruit availability was drastically different for both years of the study. This is the first report of this species as a host of *A. suspensa.* This species is probably extremely rare on the island.

Coffea arabica is widespread and fruits between September and December every year, although some ripe fruit may be found throughout the year. Although we reared *A. suspensa* from *C. arabica*, it is unlikely that ripe coffee berries are available to fruit flies very long because fruit are usually harvested very soon after ripening. Coffee was not reported as a host to *A. obliqua* or *A. suspensa* by Seín (1933) or Martorell (1976). Coffee is recorded as a host of *A. obliqua* (Eskafi and Cunningham 1987, Souza et al. 2005). Indeed, in Brazil, various *Anastrepha* spp. have become an economic problem, with infestations resulting in premature drop of fruit and lowering the quality of beans (Souza et al. 2005).

Dovyalis caffra and its close relative, *D. hebecarpa* Warb., are reported to be relatively rare in Puerto Rico (Martorell 1976). There is no prior record of this fruit hosting *Anastrepha* spp. in Puerto Rico. Swanson and Baranowski (1972) reported this fruit as a host of *A. suspensa.*

Citrus sinensis and other species of citrus are widespread on the island except in the arid south. Seín (1933) reports that *C. sinensis*, among many other *Citrus* spp., is an "occasional" host of *A. suspensa.*

Anacardium occidentale is a tree associated with dwellings in Puerto Rico, but it is unclear how widespread it is. *A. occidentale* is reported as a host of *A. obliqua* in Puerto Rico by Martorell (1976) and elsewhere (Stone 1942, Korytkowski and Ojeda Peña 1970, Wasbauer 1972, Eskafi and Cunningham 1987, Fernández et al. 1998).

Spondias mombin, S. purpurea, and *Psidium guajava* appeared to yield noticeably larger numbers of pupae per kilogram in 2006 than in 2005. At least for the two *Spondias* species, this may reflect the fact that mango trees appeared to have many more fruit in 2005 than in 2006, thus reducing the incidence of *A. obliqua* in alternate hosts. Collections of other fruits were too few to provide adequate comparisons between the years.

Intriguing discrepancies were revealed between the literature of reported hosts and direct observations in Puerto Rico. An extensive literature reports 91 plant species from 26 families as hosts of *A. obliqua* and 97 plant species from 27 families as hosts of *A. suspensa* (Norrbom 2004). Forty-five species (representing 21 families) of the reported hosts for *A. obliqua* and 50 species (representing 22 families) of the reported hosts for *A. suspensa* are listed among the flora of Puerto Rico (Liogier 1985, 1988, 1994, 1995, 1997, Norrbom 2004). The extensive survey of the literature of Martorell (1976) pertaining to Puerto Rican insect host records and museum specimens revealed 6 host species (representing two families) for *A. obliqua* and 15 host species (representing eight families) for *A. suspensa.* Surveys of fruit fly hosts in Puerto Rico may not have been exhaustive, but the scale of the discrepancy between reported hosts occurring in Puerto Rico and the number of hosts reported in the Puerto Rican literature suggests that not all plants that are reported to be hosts to *A. obliqua* and *A. suspensa* are hosts in Puerto Rico. *C. arabica* is reported to be a host of *A. obliqua* (Eskafi and Cunningham 1987), but we only recovered *A. suspensa* from this host, which is not reported in any literature, including Martorell's survey. We would expect that coffee, a historically important and widespread crop in Puerto Rico, would have been surveyed for fruit fly infestations, although this is not necessarily the case. However, the extremely low rate of infestation we observed (17 pupae from 1,283 fruit) may account for the fact that *C. arabica* was not previously reported as a host. Although *E. uniflora* is reported from a variety of regions to be a host for both species (McAlister 1936, Stone 1942, Weems 1965, Swanson and Baranowski 1972, Windeguth et al. 1972, Aluja 1984, Eskafi 1990, Cou-
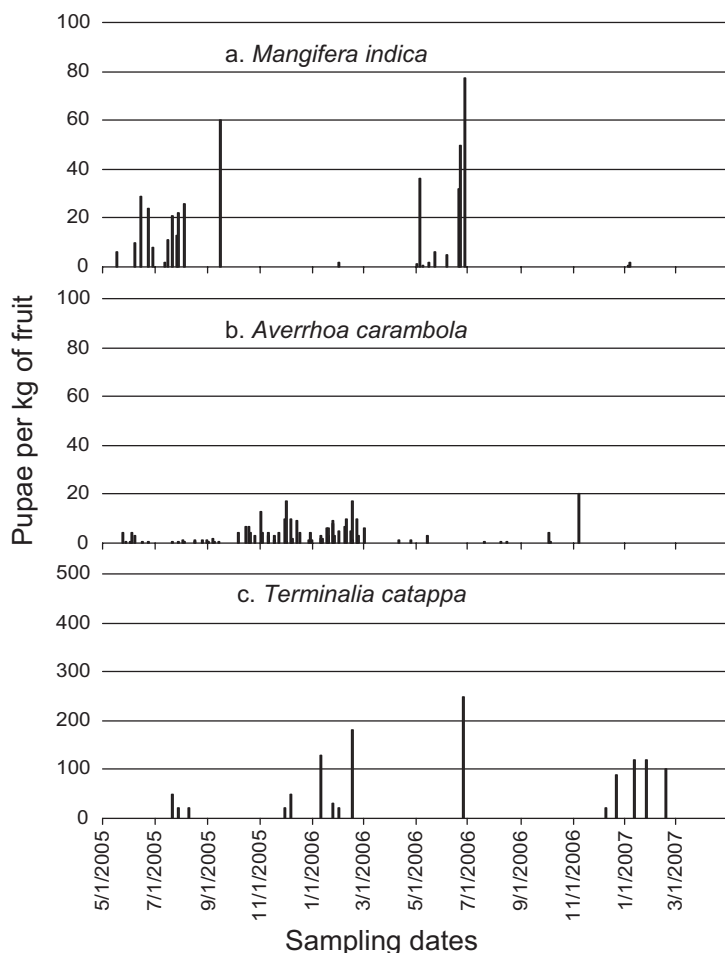
Fig. 5. Pupae per kilogram of fruit for (a) *M. indica*, (b) *A. carambola*, and (c) *T. catappa* between May 2005 and May 2007.

turier et al. 1993, Silva et al. 1996, Fernández et al. 1998, Souza Filho et al. 2000, Veloso et al. 2000). Martorell (1976) and Seín (1933) did not report it as a host for either species. We recovered 363 pupae and 239 adult *A. suspensa* from 659 fruit. Although a number of reports list both *Anastrepha* species as infesting *Citrus* spp. (McAlister 1936, Stone 1942, Korytkowski and Ojeda Peña 1970, Swanson and Baranowski 1972, Wasbauer 1972, Martorell 1976, Eskafi and Cunningham 1987, Bressan and da Costa Teles 1991, Aguiar-Menezes and Menezes 1997), Martorell (1976) and Seín (1933) only report evidence that *A. suspensa* infests citrus in Puerto Rico. We only recovered four pupae (only one of which became an adult and was identified as *A. obliqua*) from 203 fruit. Finally, *A. carambola* is reported as a host of *A. suspensa* (Swanson and Baranowski 1972), but we never recovered adult *A. suspensa* from >3,800 fruit, despite the fact that *A. suspensa* was commonly found in Multilure traps baited with putrescine and ammonium acetate (Biolure; Suterra, Bend, OR) that were placed in carambola orchards (unpublished data).

There also seems to be a striking discrepancy between the data we collected pertaining to *M. zapota* and trials with baited traps in Puerto Rican orchards of *M. zapota.* Pingel et al. (2006) reported relatively high numbers (20 flies per trap per day) of *Anastrepha* spp. (>99% *A. suspensa*) in an orchard of *M. zapota,* suggesting that these flies were attracted to this fruit. We were only able to rear one tephritid pupae from 258 *M. zapota* fruit. There are a number of possible explanations for this apparent discrepancy: the earlier study (Pingel et al. 2006) was conducted in Santa Isabel in the southern part of Puerto Rico, whereas all of our fruit was collected from Isabela, on the northwest coast of the island; unlike the other fruit we collected, mature fruit of *M. zapota* was harvested directly from the tree and so may not have had time to become infested. The orchard we sampled from was young and only began to produce appreciable numbers of fruit in 2007.

The phenomenon of "host switching" is apparent in the case of fruit flies infesting *A. carambola.* Trees of this crop can have fruit available throughout the year,
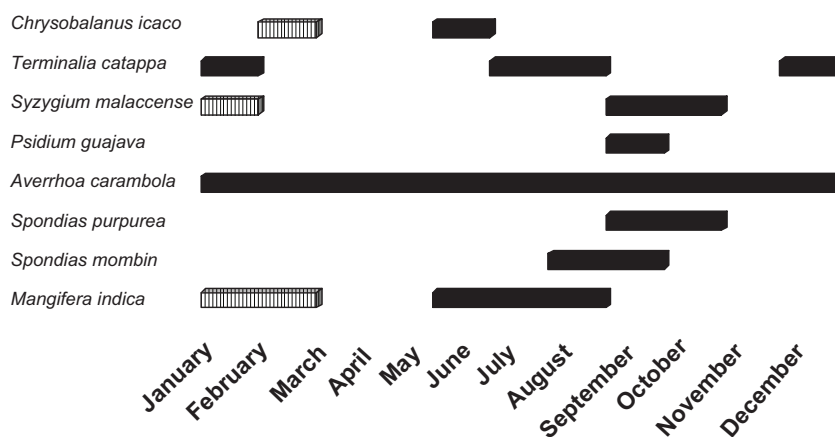
Fig. 6. Phenologies of host fruit availability. Hatched bars indicate reduced availability, either through lower yields per tree or only a small proportion of trees fruiting.

and in all seasons, some fruit may be found that are infested with *A. obliqua.* However, the extent of infestation (pupae per kilogram of fruit) is statistically different at different times of the year; in March through September, the numbers of *A. obliqua* pupae are significantly lower than in the other months. This period coincides with the availability primarily of mango fruit and fruit of *S. purpurea* and *S. mombin,* as well many other fruits that are usually heavily infested by *A. obliqua* (Fig. 5).

We observed a low level of parasitism (0.3% of pupae yielded parasitoids) by only one species of parasitoid (not including the single specimen of the introduced *D. areolatus* that we recovered). We do note that we collected >1,000 tephritid pupae from a single tree of *S. mombin* located in Mayaguez, every one of which was infested with *U. anastrephae* (unpublished data)! *U. anastrephae* seems to have a wide distribution on the island; it emerged from fruit fly pupae collected from Mayaguez, Isabela, Corozal, Adjuntas, Hatillo, and Añasco. Parasitoids were never recovered from southern districts of Puerto Rico, such as Juana Diaz and Cabo Rojo, but the overall rate of parasitism was so low that our numbers of samples may have failed to recover parasitoids that may be present at those locations in low numbers. *U. anastrephae* were recovered from *M. indica, S. mombin, P. guajava,* and *T. catappa* (Table 2). Forty-one *U. anastrephae* were collected during summer months, and five were collected during winter months. This may be a reflection of the more numerous collections of *M. indica, P. guajava,* and *S. mombin* during the summer months than winter months.

We were able to construct a tentative phenology of the observed hosts; availability of host fruit was highest in the summer rainy season, but many hosts were also available in the dry winter months (Fig. 6). The phenology of fruit availability in the tropics is complicated, but it seems that most hosts (in terms of individuals and species) are available in the summer months. There are exceptions to this rule (species or

isolated individuals within species may produce fruit in the winter or in asynchrony of their conspecifics). Of the fruits we collected that yielded *Anastrepha* pupae, *T. catappa, S. dulcis, Citrus* spp., *A. carambola, M. indica, S. mombin, S. malaccense, G. intermedia,* and *C. arabica* produced fruit in the winter, although for three of these (*M. indica, S. mombin,* and *S. malaccense*), winter fruiting was either restricted in volume of fruit produced or restricted to particular regions. Of these, citrus was only available in the winter. The others were available in the summer as well as winter.

This study reinforces the relative use of various host fruit species by *A. obliqua* and *A. suspensa.* We acknowledge that we have not exhaustively surveyed the potential hosts (i.e., plants with fleshy fruits) of *Anastrepha* spp. in Puerto Rico. Indeed, it is possible that these species use nontraditional hosts (i.e., nonfruits). This survey establishes that host-use patterns of *A. obliqua* and *A. suspensa* in Puerto Rico are inconsistent when compared with host-use patterns of these flies in other regions. Decisions pertaining to restrictions of fruit exports based on global data may be more restrictive than they need to be. What this survey does not establish is how abundant these hosts are in time and space. Future studies should also address *Anastrepha* spp. host-use patterns on the eastern half of the island.

References Cited

Aguiar-Menezes, E. L., and E. B. Menezes. 1997. Natural occurrence of parasitoids of *Anastrepha* spp. Schiner, 1868 (Diptera: Tephritidae) in different host plants, in Itaguai (RJ), Brazil. Biol. Control 8: 1–6.

Aluja, S. M. 1984. Manejo integrado de las moscas de la fruta (Diptera: Tephritidae). Direccion Gral. Sanidad Vegetal, SARH, Mexico.

Aluja, S. M., J. C. Guillen, G. de la Rosa, M. Cabrera, H. Celedonio, P. Liedo, and J. P. Hendrichs. 1987. Natural host plant survey of the economically important fruit flies (Diptera: Tephritidae) of Chiapas, Mexico. Fla. Entomol. 70: 329–338.

Aluja, S. M., J. Pinero, M. Lopez, C. Ruiz, A. Zuniga, E. Piedra, F. Diaz-Fleischer, and J. Sivinski. 2000. New host plant and distribution records in Mexico for *Anastrepha spp., Toxotrypana curvicauda* Gerstacker, *Rhagoletis zoqui* Bush, *Rhagoletis* sp., and *Hexachaeta* sp. (Diptera: Tephritidae). Proc. Entomol. Soc. Wash. 102: 802–815.

American Phytopathological Society. 1998. Mango, pp. 33–40. *In* R. C. Ploetz, G. A. Zentmyer, W. T. Nishijima, K. G. Rohrbach, and H. D. Ohr (eds.), Compendium of tropical diseases. APS Press, St. Paul, MN.

Araujo, E. L., J. L. Batista, and R. A. Zucchi. 2000. Moscas-das-frutas nos estados brasileiros. Paraíba, pp. 227–228. *In* A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento básico e aplicado, Holos, Riberão Preto.

Boscán de Martínez, N., J. R. Dedordy, and J. R. Requena. 1980. Estado actual de la distribucion geografica y hospederas de *Anastrepha* spp. (Diptera-Trypetidae) en Venezuela. Agron. Trop. (Maracay) 30: 55–63.

Boykin, L. M., R. G. Shatters, Jr., D. G. Hall, R. E. Burns, and R. A. Franqui. 2006. Analysis of host preference and geographical distribution of *Anastrepha suspensa* (Diptera: Tephritidae) using phylogenetic analyses of mitochondrial cytochrome oxidase I DNA sequence data. Bull. Entomol. Res. 96: 457–469.

Bressan, S., and M. da Costa Teles. 1991. Lista de hospedeiros e índices de infestatação de algumas espécies do gênero *Anastrepha* Schiner, 1868 (Diptera: Tephritidae) na região de Ribeirão Preto-SP. Ann. Soc. Entomol. Bras. 20: 5–15.

Carroll, L. E., I. M. White, A. Freidberg, A. L. Norrbom, M. J. Dallwitz, and F. C. Thompson. 2002 Pest fruit flies of the world (http://delta-intkey.com).

Couturier, G., R. A. Zucchi, M. G. Saravia, and N. M. da Silva. 1993. New records of fruit flies of the genus *Anastrepha* Schiner 1868 (Diptera, Tephritidae) and their host plants, in the Amazon region. Ann. Soc. Entomol. Fr. (N.S.) 29: 223–224.

Cowley, J. M., R. T. Baker, and D. S. Harte. 1992. Definition and determination of host status for multivoltine fruit fly (Diptera: Tephritidae) species. J. Econ. Entomol. 85: 312–317.

de Souza Filho, M. F., A. Raga, and R. A. Zucchi. 2000. Moscas-das-frutas nos estados brasileiros. São Paulo, pp. 277–283. *In* A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento Básico e Aplicado, Holos, Riberão Preto.

Enkerlin, D., R. L. Garcia, and M. F. Lopez. 1989. Pest status; Mexico, Central and South America, pp. 83–90. *In* A. S. Robinson and G. Hooper (eds.), Fruit flies: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands.

Epsky, N. D., P. E. Kendra, and R. L. Heath. 2003. Development of lures for the detection and delimitation of invasive *Anastrepha* fruit flies. Proc. Caribbean Food Crops Soc. 39: 84–89.

Eskafi, F. M. 1990. Parasitism of fruit flies *Ceratitis capitata* and *Anastrepha*-spp. (Diptera: Tephritidae) in Guatemala. Entomophaga 35: 355–362.

Eskafi, F. M., and R. T. Cunningham. 1987. Host plants of fruit flies (Diptera: Tephritidae) of economic importance in Guatemala. Fla. Entomol. 70: 116–123.

Fernández, A. M., D. Rodríguez, and V. Hernández-Ortiz. 1998. Notas sobre el genero *Anastrepha* Schiner en Cuba con descripcion de una nueva especie (Diptera: Tephritidae). Folia Entomol. Mex. 99: 29–36.

Haji, F.N.P., and I. da Gama Miranda. 2000. Moscas-das-frutas nos estados brasileiros. Pernambuco, pp. 229–233. *In* A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento Básico e Aplicado, Holos, Riberão Preto.

Jenkins, D. A., and R. Goenaga. 2007. Host status of mamey sapote, Pouteria sapota (Sapotaceae), to the West Indian fruit fly, *Anastrepha obliqua* (Diptera: Tephritidae) in Puerto Rico. Fla. Entomol. 90: 384–388.

Korytkowski, G.C.A., and D. Ojeda Peña. 1970. Especies del genero *Anastrepha* Schiner 1868 en el nor-oeste peruano. Rev. Peru. Entomol. 11: 32–70.

Liogier, H. A. 1985. Descriptive flora of Puerto Rico and adjacent islands. Volume I: Casuarinaceae to Connaraceae. Editorial de la Universidad de Puerto Rico, San Juan, PR.

Liogier, H. A. 1988. Descriptive flora of Puerto Rico and adjacent islands. Volume II: Leguminosae to Anacardiaceae. Editorial de la Universidad de Puerto Rico, San Juan, PR.

Liogier, H. A. 1994. Descriptive flora of Puerto Rico and adjacent islands. Volume III: Cyrillaceae to Myrtaceae. Editorial de la Universidad de Puerto Rico, San Juan, PR.

Liogier, H. A. 1995. Descriptive flora of Puerto Rico and adjacent islands. Volume IV: Melastomataceae to Lentibulariaceae. Editorial de la Universidad de Puerto Rico, San Juan, PR.

Liogier, H. A. 1997. Descriptive flora of Puerto Rico and adjacent islands. Volume V: Acanthaceae to Compositae. Editorial de la Universidad de Puerto Rico, San Juan, PR.

Martorell, L. F. 1976. Annotated food plant catalog of the insects of Puerto Rico. University of Puerto Rico, San Juan, PR.

McAlister, L. C., Jr. 1936. Observations on the West Indian fruit fly at Key West in 1932–33. J. Econ. Entomol. 29: 440–445.

Molineros, J., J. O. Tigrero, and D. Sandoval. 1992. Diagnostico de la situacion actual del problema de las moscas de la fruta en el Ecuador. Comision Ecuatoriana de Energia Atomica, Direccion de Investigaciones, Quito, Ecuador.

Morton, J. F. 1987. Fruits of warm climates. Media, Greensboro, NC.

Norrbom, A. L. 2004. Host plant database for *Anastrepha* and *Toxotrypana* (Diptera: Tephritidae: Toxotrypanini) (http://www.sel.barc.usda.gov:591/diptera/Tephritidae/TephHosts/search.html).

Oliveira, F. L., E. L. Araujo, E. F. Chagas, and R. A. Zucchi. 2000. Moscas-das-frutas nos estados brasileiros. Maranhão, pp. 211–212. *In* A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento básico e aplicado. Holos, Riberão Preto.

Pingel, R. L., N. D. Epsky, and R. Goenaga. 2006. Field trials of lures to attract fruit flies (Diptera: Tephritidae) in comercial sapodilla, mamey sapote, and carambola orchards in Puerto Rico. J. Agric. Univ. P. R. 90: 109–114.

Seín, F., Jr. 1933. *Anastrepha* (Trypetydae [sic], Diptera) fruit flies in Puerto Rico. J. Dept. Agric. P. R. 17: 183–196.

da Silva, N. M., S. Silveira Neto, and R. Zucchi. 1996. The natural host plants of *Anastrepha* in the state of Amazonas, Brazil, pp. 353–357. *In* B. A. McPheron and G. J. Steck

(eds.), Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, St. Lucia.

Souza, S.A.S., A.L.S. Resende, P. C. Strikis, J. R. Costa, M.S.F. Ricci, and E. L. Aguiar-Menezes. 2005. Infestacao natural de moscas frugivoras (Diptera: Tephritoidea) em café arabica, sob cultivo organico arborizado e a plano sol, em Valenca RJ. Neotrop. Entomol. 34: 639–648.

Steck, G. J., L. E. Carroll, H. Celedonio-Hurtado, and J. Guillen-Aguilar. 1990. Methods for identification of Anastrepha pupae (Diptera: Tephritidae), and key to 13 species. Proc. Entomol. Soc. Wash. 92: 333–346.

Stone, A. 1942. The fruitflies of the genus Anastrepha. USDA misc. publ. 439, 112 pp.

Swanson, R. W., and R. M. Baranowski. 1972. Host range and infestation by the Caribbean fruit fly, Anastrepha suspensa (Diptera: Tephritidae), in south Florida. Proc. Fla. State Hortic. Soc. 1972: 271–273.

Uchôa, F.M.A., and R. A. Zucchi. 2000. Moscas-das-frutas nos estados brasileiros. Mato Grosso e Mato Grosso do Sul, pp. 241–245. In A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento Básico e Aplicado, Holos, Riberão Preto.

Uchôa, F.M.A., I. de Oliveira, R.M.S. Molina, and R. A. Zucchi. 2002. Species diversity of frugivorous flies (Diptera: Tephritoidea) from hosts in the cerrado of the state of Mato Grosso do Sul, Brazil. Neotrop. Entomol. 31: 515–524.

van Whervin, L. W. 1974. Some fruitflies (Tephritidae) in Jamaica. Pest Articles and News Summaries 20: 11–19.

Veloso, V.R.S., P. M. Fernandes, and R. A. Zucchi. 2000. Moscas-das-frutas nos estados brasileiros. Goiás, pp. 247–252. In A. Malavasi and R. A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil. Conhecimento Básico e Aplicado, Holos, Riberão Preto.

von Windeguth, D. L., W. H. Pierce, and L. F. Steiner. 1972. Infestations of Anastrepha suspensa in fruit on Key West, Florida. Fla. Entomol. 56: 127–131.

Wasbauer, M. S. 1972. An annotated host catalogo f the fruit flies of America North of Mexico (Diptera: Tephritidae). Occas. Pap. Calif. Dept. Agric. Bur. Entomol. 19: 172.

Weems, H. V., Jr. 1965. Anastrepha suspensa (Loew) (Diptera: Tephritidae). Fla. Dep. Agric. Div. Plant Industry, Entomol. Circ. 38: 4.

White, I. M., and M. M. Elson-Harris. 1992. Fruit flies of economic significance: their identification and bionomics. CAB International, Wallingford, Oxon, UK.

Wolcott, G. N. 1948. The insects of Puerto Rico. J. Agric. Univ. P. R. 32: 508–511.